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Gastropods slow down succession and maintain diversity in cryptogam communities

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Abstract. Herbivore effects on diversity and succession were often studied in plants, but not in cryptogams. Besides direct herbivore effects on cryptogams, we expected indirect effects by changes in competitive interactions among cryptogams. Therefore, we conducted a long-term gastropod exclusion experiment testing for grazing effects on epiphytic cryptogam communities. We estimated the grazing damage, cover and diversity of cryptogams before gastropods were excluded and three and six years thereafter. Gastropod herbivory pronouncedly affected cryptogams, except for bryophytes, strongly depending on host tree species and duration of gastropod exclusion. On control trees, gastropod grazing regulated the growth of algae and non-lichenized fungi and thereby maintained a high lichen diversity and cover. On European beech, the release from gastropod grazing temporarily increased lichen vitality, cover, and species richness, but later caused rapid succession where algae and fungi overgrew lichens and thereby reduced their cover and diversity compared with the control. On Norway spruce, without gastropods lichen richness decreased and lichen cover increased compared with the control. Our findings highlight the importance of long-term exclusion experiments to disentangle short-term, direct effects from longer-term, indirect effects via changes in competitive relationships between taxa. We further demonstrated that gastropod feeding maintains the diversity of cryptogam communities.

Key words: *algae; biodiversity; bryophyte; epiphyte; lichenized fungi; gastropod grazing; rapid succession; top-down regulation.*

INTRODUCTION

Herbivory can affect local plant community structure, species richness, species distributions, ecosystem dynamics and succession (Crawley 1997). Underlying processes involve the reduction of competitive interactions and plant homogenization by the consumption of dominant or nutritious species, alteration of colonization-extinction dynamics by zoochorous propagule dispersal or removal and increase of spatial heterogeneity by the creation of colonizable gaps through disturbances (Crawley 1997, Olff and Ritchie 1998). However, the underlying mechanisms may depend on the type, size, and selectivity of herbivores (Crawley 1997, Bakker et al. 2006), grazing pressure (Proulx and Mazumder 1998), temporal variation in grazing intensity (increased diversity with increased temporal variation; Allan et al. 2014), and variation among environmental conditions (e.g., resource availability; Proulx and Mazumder 1998,

Bakker et al. 2006). As all these mechanisms can have cumulative, interactive, or compensatory effects, and as they can vary among functional groups, the main direction of herbivore effects on species richness can therefore be positive, neutral, or negative (Olff and Ritchie 1998, Allan and Crawley 2011).

Non-fern cryptogam communities are composed of algae, bryophytes, cyanobacteria, non-lichenized fungi (further referred as fungi), and lichens and occur in essentially all terrestrial and aquatic habitats where they are frequently grazed by various animals including gastropods (Davidson et al. 1990, Speiser 2001, Hillebrand 2003, Glime 2013). However, effects of herbivory on species richness, abundance, and composition of such cryptogams have been studied only very rarely, and the few existing studies mainly considered effects on single species of one cryptogam taxon (Asplund et al. 2010) or interacting effects between two cryptogam taxa (Fröberg et al. 2011). Moreover, although some studies demonstrated synergistic interactions (e.g., positive grazing effects on endolithic lichens by the release from cyanobacteria and epilithic lichens: Fröberg et al. 2011,

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dispersal of bryophytes and lichens: Boch et al. 2011, 2013a, 2015a), the relationship between gastropods and cryptogams has mainly been considered to be antagonistic (e.g., limiting effects on *Lobaria pulmonaria* establishment; Asplund and Gauslaa 2008). However, despite high gastropod densities and grazing pressures in many forests, especially of slugs consuming large quantities, grazing effects on species richness and composition within and across epiphytic cryptogam taxa have only rarely been tested.

In cryptogam communities, competition within and between taxa can have effects on species richness and composition. On trees, for example, dominant bryophyte and large foliose lichen species have been shown to out-compete small foliose and crustose lichen species (reviewed in Ellis 2012). Transferring results from seed plants, we expect that grazing animals, in addition to direct effects on cryptogams, may indirectly change competitive interactions among cryptogams and create gaps for colonization by other species. Moreover, also in cryptogam communities, the biomass removal by herbivores might enhance the diversity of bryophytes and lichens because of competitive release of slow growing and of pioneer species from fast growing and dominant ones, including fungi and algae. To date, it has not been experimentally tested whether herbivores, such as gastropods, can alter these competitive relationships among cryptogams and whether grazing effects are consistent among tree species.

To study herbivore effects on species richness and community composition of cryptogams, few exclusion experiments have been carried out (mostly over short time periods, however). Examples include reindeer exclusion (den Herder et al. 2003) or gastropod exclusion in both marine (Hillebrand 2003) and terrestrial systems (Rosso and McCune 2003, Asplund and Gauslaa 2008). Given the slow growth of many cryptogams, however, the effect of grazing may well change over time, because altered competitive interactions among cryptogams require time to become manifested.

We present a long-term experiment in which we studied the response of epiphytic cryptogam communities, including algae, bryophytes, fungi and lichens, to gastropod grazing. In particular, we excluded gastropods from the trunks of two tree species, European beech and Norway spruce, over six years and then compared how the grazing damage and the cover and diversity of cryptogams changed compared to control trees with gastropods present. Thereby we sought to test the hypotheses that (1) gastropods are important herbivores in epiphytic cryptogam communities on tree stems, and the release of gastropod grazing will strongly reduce the grazing damage on bryophytes and lichens, and (2) in line with the well-established findings from seed plants, gastropod herbivory, in cryptogam communities is important because it regulates competitive relationships within and among cryptogam taxa and thereby maintains the diversity in cryptogam communities.

MATERIALS AND METHODS

Study system

This study was conducted as part of the Biodiversity Exploratories project (Fischer et al. 2010; www.biodiversity-exploratories.de) in the UNESCO Biosphere area Schwäbische Alb. This low mountain range is situated in south-west Germany (48°20'60.0"–48°32'3.7" N; 9°12'13.0"–9°34'48.9" E) and formed by calcareous bedrock. Mean annual precipitation of the study region ranges from 700 to 1,000 mm and mean annual temperature is 6–7°C. The forests in the study region are largely dominated by European beech (*Fagus sylvatica* L.) or Norway spruce (*Picea abies* (L.) H. Karst.), harbor diverse epiphytic bryophyte and lichen communities (Boch et al. 2013b, c), and various cryptogam-eating gastropods comprising slug species (e.g., *Arion* spp., *Deroceras* spp., *Limax cinereoniger*) and snail species (e.g., *Cepaea* spp., *Ena montana*, *Helicodonta obvolvata*, and many species of the Clausilidae family; see also Boch et al. 2011, 2013a, 2015a, b).

Experimental setup

In April 2008, we selected a subset of nine plots (20 × 20 m) out of the Biodiversity Exploratories forest plots, which are dedicated to intensive research. The plots were all situated in similar altitudes ranging from 690 to 790 m a.s.l. As one of our sampling trees was destroyed by a lightning in 2010, we excluded the plot from the analysis, resulting in a total number of eight plots. Three plots contained pure Norway spruce stands and five stands were dominated by European beech. On each plot, we then selected one pair of trees with a similar diameter. On each tree we placed a vertical transect subdivided into five 10 × 10 cm subplots at all four expositions of the tree trunk and permanently marked the four areas per tree with a staple gun using corrosion-free aluminum staples (8 plots × 2 trees × 4 expositions × 5 subplots = 320 subplots in total). On one tree per pair of trees per plot, we then excluded gastropods by applying a 10 cm broad barrier of gastropod-repellent paste (IRKA Schneckenabwehrpaste; R+M Gartenbedarf GbR, Rehling, Germany) at tree base. This paraffin-based paste contains only non-toxic compounds, according to manufacturer information, and has already been successfully used to exclude or enclose gastropods (Türke et al. 2012, Boch et al. 2015a) without harming other organisms. The paste was applied twice per year in March/April and again in June from 2008 to 2014. As gastropods overwinter on or in the ground, applying the paste in March/April, when gastropod activity is only beginning prevents them from climbing the trees. Applying paste again in June ensured permanent gastropod exclusion. In April 2008, before the exclusion, and in April 2011 and 2014, we recorded the percentage cover of all lichen and bryophyte species as well as the total cover of free living green algae in each

TABLE 1. ANOVA results for the differences between tree species, treatments, and expositions in the change of grazing damage of lichens, lichen species richness, and cover between the sampling dates.

	df	Lichen herbivory						Lichen species richness						Lichen cover					
		2008 vs. 2011		2011 vs. 2014		2008 vs. 2014		2008 vs. 2011		2011 vs. 2014		2008 vs. 2014		2008 vs. 2011		2011 vs. 2014		2008 vs. 2014	
		t/F	P/MS	t/F	P/MS	t/F	P/MS	t/F	P/MS	t/F	P/MS	t/F	P/MS	t/F	P/MS	t/F	P/MS	t/F	P/MS
Overall mean change	1	-9.2	<0.001	-3.7	<0.001	-10.2	<0.001	8.6	<0.001	2.7	0.007	9.3	<0.001	4.2	<0.001	-1.9	0.059	0.3	0.758
Error: plot																			
Tree species	1	9.9	0.020	2.3	0.181	10.6	0.018	0.2	0.665	4.4	0.080	2.1	0.195	0.0	0.911	9.0	0.024	9.0	0.024
Residuals MS	6		1,357.0		107.0		1,639.0		2.7		4.2		6.0		248.9		869.0		907.0
Error: plot × tree individual																			
Treatment (Treat.)	1	23.3	0.003	1.2	0.315	47.4	<0.001	10.2	0.019	58.6	<0.001	23.9	0.003	1.1	0.343	7.0	0.039	7.4	0.035
Tree sp. × treat.	1	10.3	0.018	0.7	0.430	21.4	0.004	4.4	0.080	9.6	0.021	1.7	0.235	0.7	0.448	7.4	0.035	4.5	0.079
Residuals MS	6		1,594.0		140.8		895.0		1.6		2.3		2.4		173.7		1,030.0		1,313.0
Error: plot × tree individual × transect																			
Exposition (Exp.)	3	0.5	0.675	2.3	0.093	1.1	0.373	0.9	0.438	2.2	0.105	1.0	0.406	0.2	0.929	1.8	0.169	1.3	0.282
Tree sp. × exp.	3	0.4	0.720	1.2	0.318	0.8	0.497	0.7	0.555	0.5	0.660	1.0	0.405	0.2	0.904	0.5	0.654	0.8	0.509
Treat. × exp.	3	0.4	0.737	1.8	0.171	0.6	0.651	0.5	0.705	0.4	0.755	0.3	0.809	3.1	0.037	0.4	0.780	1.9	0.144
Tree sp. × treat. × exp.	3	0.5	0.689	1.1	0.368	0.5	0.654	1.0	0.408	0.3	0.842	1.0	0.392	0.5	0.713	0.6	0.621	0.7	0.578
Residuals MS	36		565.9		194.9		821.0		1.9		2.9		3.6		78.9		257.8		282.7
Error: within																			
Residuals MS	256		160.3		50.7		138.1		0.8		0.7		1.048		43.3		60.4		84.7

Note: Significant differences are indicated by bold *P*-values.

subplot. Moreover, we estimated the grazing damage by gastropods as percentage of grazed area for each lichen and bryophyte species. In 2011, we noticed the fungus species *Arthopyrenia punctiformis* which we probably overlooked in 2008 because its thallus mainly grows inside the bark of European beech and its fruiting bodies, which grow on the surface of the bark, were generally heavily grazed with gastropods present. Thus, we possibly underestimated fungus cover in 2008 and therefore only used the cover values from 2011 and 2014.

Statistical analysis

We analyzed the change of cover by lichens, bryophytes, algae, and fungi, the change in lichen and bryophyte species richness, as well as the change in grazing damage on bryophytes and lichens as recorded at the 10 × 10 cm subplot scale. To do so we used a split-plot analysis of variance (ANOVA) in R, Version 3.1.0 (R Development Core Team 2014) including the effects of tree species, gastropod exclusion and exposition. We calculated separate models for the changes from 2008 to 2011, 2011 to 2014, and 2008 to 2014, respectively. Models contained terms for tree species (Norway spruce or European beech), treatment (two levels: gastropod exclusion/control) and exposition (N, E, S, W) and their interactions as well as the nested

random effects of eight plots, two trees per plot and four transects per tree, using the function `aov()` in R:

$y \sim \text{tree species} \times \text{treatment} \times \text{exposition} + \text{Error}(\text{plot/tree/transect}).$

Sequential *F*-tests were used to test the significance of changes in cover and richness due to factors added progressively to the model (the sequence is shown in Tables 1 and 2).

To analyze temporal changes in species composition of cryptogam taxa between the treatments, we performed a nonmetric multidimensional (MDS) ordination (Appendix S1: Fig. S1, Table S1). Data were squared-root transformed to reduce excessive influence of dominant species. Stress values of the 2D MDS ordination were 0.17 for *F. sylvatica* and 0.05 for *P. abies*, indicating that two axes already well captured the differences in species composition. MDS ordinations were carried out in Primer v.6 statistical package (PRIMER-E Ltd., Plymouth Marine Laboratory, Plymouth, UK).

RESULTS

Grazing damage of lichens and bryophytes

At the start of the experiment, the percentage of grazed lichen area was much higher on European beech

TABLE 2. ANOVA results for the differences between tree species, treatments, and expositions in the change of bryophyte species richness and cover by bryophytes, algae, and fungi between the sampling dates.

	df	Bryophyte species richness						Bryophyte cover						Algal cover						Fungal cover	
		2008 vs. 2011		2011 vs. 2014		2008 vs. 2014		2008 vs. 2011		2011 vs. 2014		2008 vs. 2014		2008 vs. 2011		2011 vs. 2014		2008 vs. 2014		2011 vs. 2014	
		t/F	P/MS	t/F	P/MS	t/F	P/MS	t/F	P/MS	t/F	P/MS	t/F	P/MS	t/F	P/MS	t/F	P/MS	t/F	P/MS	t/F	P/MS
Overall mean change	1	4.5	<0.001	5.3	<0.001	6.0	<0.001	3.4	<0.001	3.6	<0.001	3.6	<0.001	5.4	<0.001	4.6	<0.001	6.1	<0.001	4.4	<0.001
Error: plot																					
Tree sp.	1	1.4	0.280	0.8	0.409	1.0	0.351	0.8	0.410	0.7	0.435	0.7	0.428	0.6	0.479	1.5	0.261	0.8	0.399	3.9	0.097
Residuals MS	6		1.0		1.6		5.2		63.3		597.9		1,049.5		5,141.0		127.0		5,795.0		485.2
Error: plot × tree individual																					
Treatment (Treat.)	1	1.2	0.316	0.0	0.934	0.4	0.560	1.2	0.313	1.3	0.302	1.3	0.304	3.1	0.127	11.0	0.016	6.1	0.049	4.9	0.069
Tree sp. × treat.	1	0.0	0.928	0.2	0.657	0.1	0.784	0.7	0.444	0.7	0.433	0.7	0.435	1.9	0.222	3.7	0.103	2.8	0.144	2.9	0.137
Residuals MS	6		0.2		0.4		0.8		47.6		397.7		719.8		3,260.0		557.0		5,384.0		1,831.0
Error: plot × tree individual × transect																					
Exposition (exp.)	3	0.3	0.814	0.4	0.736	0.4	0.748	1.1	0.366	1.3	0.287	1.3	0.305	0.9	0.445	1.3	0.276	1.0	0.408	0.8	0.517
Tree sp. × exp.	3	0.6	0.622	0.4	0.739	0.8	0.496	0.6	0.593	0.8	0.489	0.8	0.513	0.3	0.839	0.6	0.595	0.3	0.842	0.5	0.707
Treat. × exp.	3	1.2	0.318	0.4	0.725	0.1	0.970	0.9	0.432	0.8	0.514	0.8	0.494	0.4	0.785	0.1	0.933	0.2	0.881	0.4	0.739
Tree sp. × treat. × exp.	3	0.3	0.792	0.2	0.926	0.0	0.996	0.6	0.651	0.5	0.693	0.5	0.682	0.2	0.910	0.3	0.853	0.1	0.955	0.3	0.856
Residuals MS	36		0.2		0.5		1.5		22.7		219.3		382.3		252.5		149.1		233.3		389.9
Error: within																					
Residuals MS	256		0.172		0.1		0.3		2.5		6.1		11.6		23.5		11.87		26.32		29.8

Note: Significant differences are indicated by bold *P*-values.

(33.5% ± 1.4 SE of the total lichen area) than on Norway spruce (4.7% ± 0.2). On control trees, the percentage of grazed lichen area remained essentially the same after three and six years (Fig. 1A, Table 1). In contrast, on trees where gastropods had been excluded, the grazed lichen area was reduced to 4.3% (±0.5) in 2011 and 0.7% (±0.1) in 2014 on European beech and to 0.7% (±0.1) in 2011 and 0% in 2014 on Norway spruce. This reduction of gastropod feeding was clearly visible in the field because lichen thalli were well recovered and produced many fruiting bodies. The stronger reduction of grazed lichen area on European beech than on Norway spruce, as indicated by a significant tree species × treatment interaction, was due to the absolute differences in grazed lichen area among the tree species (while percentage-wise it was very similar: 88.2% on European beech vs. 85.6% on Norway spruce; Fig. 1A). In contrast to lichens, bryophyte gametophytes showed no signs of gastropod grazing, but their diversity and cover slightly increased over time. These results indicate that the slug-repellent paste effectively excluded gastropods and is therefore suitable for long-term exclusion experiments.

Short-term gastropod effects

After three years, the richness of lichen species increased on average by 21% per subplot (mean ± SE 2008 vs. 2011:

2.25 ± 0.1 vs. 2.73 ± 0.1 species). While the increase was higher in subplots where gastropods had been excluded than in the controls (31% vs. 13%; Table 1, Fig. 1B), it did not differ among tree species. In contrast to lichen richness, the cover of lichens, the richness and cover of bryophytes as well as the cover of algae did not differ between treatments and tree species. The exposition of subplots almost never affected any variable (Tables 1 and 2). Thus, in this early stage of investigation our results suggested an antagonistic herbivorous relationship between gastropods and lichens, at least concerning their effect on lichen diversity.

Longer-term gastropod effects

In the following three years (2011–2014), bryophytes remained unaffected by the treatments. However, the effect of the gastropod exclusion on lichens differed among tree species: on Norway spruce the richness of lichen species further increased by 47% with gastropods present (mean ± SE 2011 vs. 2014: 1.72 ± 0.1 vs. 2.53 ± 0.1 species) whereas it increased only by 11% where gastropods had been excluded (2011 vs. 2014: 1.90 ± 0.1 vs. 2.10 ± 0.1 species; Fig. 1B). Interestingly, on European beech the richness of lichen species increased by 30% with gastropods present (2011 vs. 2014: 2.85 ± 0.1 vs. 3.71 ± 0.2 species) but drastically declined without gastropods by

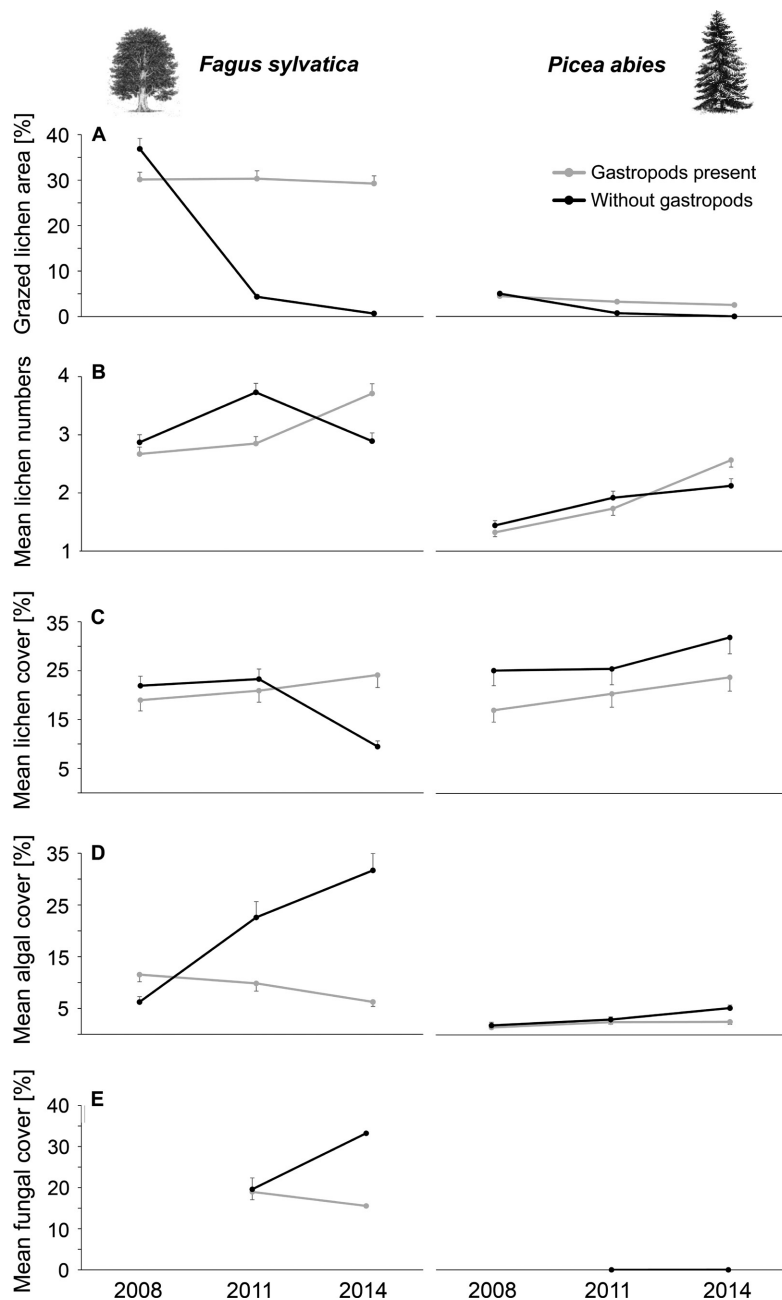


FIG. 1. Changes in (A) mean percentage of grazed lichen area (\pm SE), (B) mean lichen species richness (\pm SE), (C) mean percentage lichen cover (\pm SE), (D) mean percentage algal cover, and (E) mean percentage fungal cover (\pm SE) on European beech (*Fagus sylvatica*; left) and Norway spruce (*Picea abies*; right) among the three sampling dates separated by the control (grey line) and the gastropod exclusion treatment (black line).

23%, i.e., almost returned to the initial value we had recorded in 2008 (2011 vs. 2014: 3.73 ± 0.2 vs. 2.89 ± 0.1 species; Fig. 1B). In addition, on Norway spruce, the cover of lichens slightly increased in both treatments, whereas on European beech it slightly increased when gastropods were present, but strongly decreased by 59% without gastropods. This reduction on European beech resulted in a 43% lower cover of lichens than the initial

value from 2008 (2008 vs. 2011 vs. 2014: 21.93 ± 1.5 vs. 23.3 ± 2.1 vs. 9.50 ± 1.1 ; Table 1, Fig. 1C).

The cover of algae remained similar with gastropods present, while it was approximately five times higher in 2014 than 2008 when gastropods were excluded, especially on European beech (2008 vs. 2014: 4.6 ± 0.7 vs. 21.8 ± 2.4 ; Table 2, Fig. 1D). Similar to algae, the cover by fungi increased by 70% from 2011 to 2014 when

gastropods were excluded on European beech (2011 vs. 2014: $19.6\% \pm 2.4$ vs. $33.3\% \pm 2.8$ area covered; Fig. 1E; marginally significant Table 2).

By the end of the experiment, on European beech formerly abundant crustose lichens (e.g., *Arthonia* spp., *Graphis scripta*, *Lecanora* spp., *Lecidella elaeochroma*, *Pertusaria leioplaca*; Appendix S1: Fig. S1, Table S1) were visibly dying because they were overgrown by algae. Moreover, the fungi *Arthopyrenia punctiformis* and to a lesser degree *Ascodichaena rugosa* became dominant. Both fungi grew below the crustose lichens and often pierced fruiting bodies through the lichen thalli. On Norway spruce, the exclusion of gastropods changed the composition of lichen species and led to a cover increase of pioneer or competitive species (e.g., *Hypogymnia physodes*, *Lepraria incana*, *Micarea prasina*; Appendix S1: Fig. S1, Table S1). Overall, our findings indicate that gastropod grazing has regulating effects because it reduces the competition between taxa and thereby prevents rapid successional changes in cryptogam communities and maintains their diversity.

DISCUSSION

Grazing damage

Overall, our findings indicate that gastropods are important grazers of lichens, which is in line with the conclusions of other studies (Asplund et al. 2010, Fröberg et al. 2011). The higher percentage of grazed lichen area on European beech than on Norway spruce is likely due to different gastropod densities. However, as our plots contained either pure European beech or pure Norway spruce stands, we cannot separate the effect of forest type from the one of tree species. Martin and Sommer (2004) pointed out the importance of stand continuity for gastropod species richness and density. As all Norway spruce stands in the study region are plantations, the low overall lichen grazing damage may have resulted from a long-term legacy effect by interrupting forest continuity through clear cuts, which reduces population recovery of dispersal limited taxa such as gastropods. To corroborate this explanation, direct measurements of gastropod densities would be required. Moreover, we cannot separate the forest effect from a potential tree species effect per se. Possibly the differences in grazing damage we found between Norway spruce and European beech might be attributed to differing tree characteristics, and thus might remain when sampling spruce trees in beech stands and vice versa. However, this needs further evaluation in future studies.

More importantly, in both forest types, lichens quickly regenerated without gastropod grazing, and the signs of grazing almost disappeared after six years of gastropod exclusion while it remained similar in the controls. This corresponds to the findings of Fröberg et al. (2006), who exposed stones covered with grazed lichens in an open

area where no lichen feeders occurred and found a complete regeneration of heavily grazed lichens after three years. Similarly, Rosso and McCune (2003) found that lichens regenerated quickly after excluding gastropods from *Acer circinatum* branches by comparing cut and disconnected branches with uncut and connected ones. However, their exclusion experiment lasted only 2 yrs because the cut branches started to rot. In contrast to lichens, bryophyte gametophytes showed no signs of gastropod grazing. Gastropods have been observed to frequently graze the sporophytes and especially the green capsules of bryophytes, however, the leafy shoots (gametophytes) are only rarely grazed (reviewed in Glime 2013). Thus, our study showed that the gastropod-repellent paste is a well-suited, time and cost efficient method to exclude gastropods, even for longer time periods without harming the studied organisms. In summary, these findings partly confirm our first hypothesis that gastropods are the main herbivores in epiphytic cryptogam communities on tree stems, as the release of gastropod grazing strongly reduces the grazing damage on lichens, while bryophytes largely remain unaffected.

Gastropod effects on richness, cover and competition among epiphytic cryptogams

Overall, the richness of lichens and bryophytes increased over time. However, we found strongly contrasting patterns between short- and long-term effects of gastropod exclusion on European beech. After the first 3 yrs of the experiment, we found a higher increase of lichen richness when gastropods had been excluded than in the controls, which indicated that gastropods impair the establishment of new lichen species. This supports the findings of Asplund and Gauslaa (2008), who showed that gastropod grazing can limit early developmental stages of lichens. However, over the second 3-yr period of our experiment, the cover and richness of lichens strongly decreased while the cover of algae and fungi strongly increased when gastropods were excluded. By 2014, crustose lichens were either overgrown by algae or pushed away from the substrate by fungi growing below them. On Norway spruce, where no such pronounced increase of algal or fungal growth occurred, the exclusion of gastropods changed the composition rather than the richness of lichen species because of an increasing cover of pioneer or competitive lichens species. This is in line with Fröberg et al. (2011) who compared cyanobacterial abundance and richness of functional lichen groups along limestone cracks with and without snails on the island of Öland (Sweden). They found that snails released endolithic lichens (species living inside rocks) from light competition by grazing on cyanobacteria and epilithic lichens (species living on rocks). Taken together, these results indicate that gastropod grazing exhibits an indirect positive effect on lichens by preventing competitive exclusion of lichens by algae, fungi, or other fast growing

lichens, and thus confirms our second hypothesis. However, this was not true in bryophytes, as we found, in line with Rosso and McCune (2003), their richness and cover unaffected by gastropod feeding. This may be explained by the fact that gastropods prefer lichens and green algae over bryophytes. Our observations in the field corroborate that the cover of bryophytes is only little affected by gastropod feeding.

CONCLUSIONS

Our long-term exclusion experiment highlights that the intuitive expectation of an entirely antagonistic herbivorous relationship between gastropods and non-fern cryptogams must be challenged. By changing the competitive relationships between taxa, gastropod grazing prevented rapid successional changes in cryptogam communities and thereby maintained their diversity and stability. This highlights that the well-established results from seed plants can be transferred to cryptogams, which improves our general knowledge in the less well-studied field of herbivore-cryptogam interactions. Moreover, we clearly showed that cryptogam communities are well-suited model ecosystems to study herbivore effects on various composition and diversity aspects of communities composed of different taxa. Rapid successional changes by the removal of a higher trophic level in the food-web may also occur in more complex, larger scale ecosystems regulated by herbivores, where exclusion experiments may be unfeasible. From a conservation point of view, this highlights that the loss of a single species, or of a whole taxonomic group, can lead to strong cascading effects on ecosystem dynamics, rapid compositional changes and diversity loss. Moreover, we support that exclusion experiments should run for long periods (Allan and Crawley 2011), because grazing effects may appear only after several years and therefore change conclusions from short-term studies. In our case, the main message largely reversed by the end of the experiment. We would have reported an antagonistic herbivorous relationship between gastropods and lichens if we had stopped the experiment at an early stage of investigation.

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